EVIDENCE OF SYMBIOTIC ZOOXANTHELLAE IN A RUGOSE CORAL, *SIPHONOPHRENTIS*, FROM THE DEVONIAN OF OHIO

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ABSTRACT

The evolution of zooxanthellate endosymbionts in modern coral lineages is relatively well known, originating in the Triassic with the rise of scleractinian corals. It has been suggested that this symbiotic relationship may have evolved before the Triassic, sometime in the Paleozoic. This is a study of proxy evidence for zooxanthellate endosymbionts in a species of rugose coral, *Siphonophrentis gigantea*, from the Columbus Limestone (Devonian) of Ohio, USA. X-ray Computed Tomographic (XCT) scans were conducted on 10 specimens of *Siphonophrentis* to visualize internal growth banding, reflected as density differences in skeletal material. Growth bands were measured and examined for changes in growth pattern. Measurements of growth bands showed a range of yearly growth from 3.958 mm to 15.832 mm, with an average of 8.347 mm/year. Only five of the 10 scanned specimens had measurable growth bands preserved. Of these specimens, two showed quite high growth rates, consistent with the presence of a zooxanthellate symbiont. One specimen showed a substantial, short-term disruption in growth, suggestive of a bleaching event, including loss of the zooxanthellae.

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INTRODUCTION

The purpose of this study was to identify preserved growth banding in rugose corals from the Devonian of Ohio using X-ray Computed Tomography (XCT). The growth bands could be used as proxy evidence for zooxanthellate endosymbionts, and ecological or other environmental perturbations. The primary methodological approach, use of an XCT scanner, is nondestructive and provides a detailed look at the internal structures of corals if they are well preserved. This study focuses on *Siphonophrentis gigantea* (Lesueur, 1821), the largest rugose coral known from the Devonian of Ohio (see Babcock, 1996), and its possible zooxanthellate symbiotic relationship.

Symbiosis in Holocene Corals

The dominant reef-forming corals of the Holocene belong to the order Scleractinia. These corals are hypothesized to have been evolved from an "anemone-like" ancestor that survived the Permian mass extinction (Stanley, 2003). Scleractinains first diversified in the Triassic Period (Stanley, 2003). Two ecological forms were identified by Wells (1933): hermatypic and ahermatypic corals. Hermatypic forms, which are normally colonial, are restricted to the photic zone because zooxanthellate algae (dinoflagellates) live symbiotically within the soft tissues of the corals (e.g., Wells, 1933; Benton and Harper, 2009). Ahermatypic corals are often solitary and lack zooxanthellate endosymbionts (e.g., Wells, 1933; Benton and Harper, 2009).

The evolution of a symbiotic relationship in scleractinian corals has been hypothesized to have begun in the Triassic, which is when biomineralized scleractinians first appeared (Coates & Jackson, 1987; Stanley and Swart, 1995). The endosymbiontic zooxanthellae live in a mutualistic relationship with the corals. These dinoflagellate algae live in the tentacles and mouths of cnidarians, where they recycle nutrients, accelerate the rate of calcium carbonate skeletal deposition, and provide organic carbon and nitrogen to the polyp in return for support and protection from herbivores (Stanley, 2006; Benton and Harper, 2009; LaJeunesse et al, 2009 and references therein; Rodrigues and Grottoli, 2007). Evidence of this symbiosis can be preserved in the morphology of the corals, especially internally in the growth banding (Coates & Jackson, 1987). Holocene scleractinian corals provide examples of a symbiotic relationship and indicate how a similar relationship might be manifested in fossils.

Bleaching in Holocene Corals

A major problem facing Holocene scleractinian corals is the process of bleaching (e.g., Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Lajeunesse et al., 2009; Rodrigues and Grottoli, 2007; Grottoli et al. 2014). Bleaching is a result of changes in environmental conditions such as anomalously high or low temperatures, changes in sea level, loss of light, constant light, or increased UV radiation (Brown, 1997). According to Hoegh-Guldberg (1999) and Hoegh-Guldberg et al. (2007), rising ocean temperature and ocean acidification are the largest factors affecting coral bleaching in extant scleractinians. This process involves the expelling of the zooxanthellate endosymbionts from the soft tissues of the coral (Brown, 1997: Buddemeier & Fautin, 1993; Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Lajeunesse et al., 2009; Rodrigues and Grottoli, 2007; Grottoli et al. 2014). The process of bleaching leaves the corals without any pigment derived from photosynthetic zooxanthellae. The loss of the zooxanthellae also drastically affects the corals, many of which die due to the loss of nutrients (Brown, 1987;

Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Lajeunesse et al., 2009; Rodrigues and Grottoli, 2007) or experience lower growth rates before recovering (e.g., Leder, Szmant, & Swart, 1991; Grottoli et al. 2014).

As shown by Leder et al. (1991), evidence of bleaching events are preserved in the skeletal material of corals. Growth bands, in particular, become significantly narrower during bleaching. If corals recover from bleaching, growth bands become thicker again. The recovery is explained by the reintroduction of zooxanthellae into the coral polyps from the water column (Goulet, 2007). Growth banding analysis is an excellent method for determining if bleaching had occurred within a living or fossil coral. However, bleaching is not the only factor that affects growth banding. Other factors that may cause changes in skeletal growth include temperature changes in the water column, sea level changes, and light level changes (Highsmith, 1979).

Hermatypy in Rugose Corals?

The order Rugosa comprises an extinct clade of cnidarians that includes both solitary and colonial animals. Their skeletons were constructed of calcium carbonate, presumably aragonite. They are characterized by a distinctive ontogenetic pattern: septal insertion occurs in groups of four. This pattern had led to description of rugose corals as tetracorals. Many had a conical or 'horn' shape, inspiring the common name of "horn corals". Polyps were located at one end of the corallum, and in life evidently faced into the moving water column to collect food and oxygen (Benton & Harper, 2009). Rugose corals appear in the fossil record in the Middle Ordovician (Sorauf, 2016; Benton & Harper, 2009). By the Late Ordovician they had begun to diversify (Sorauf, 2016), and in the Silurian and Devonian are among the most common of marine invertebrate fossils (e.g., Babcock, 1996). Together with tabulate corals and stromatoporoid sponges, rugose corals were major reef formers during the mid-Paleozoic (Babcock, 1996; Scrutton, 1998: Silva, Kershaw, & Boulvain, 2011).

The largest known solitary rugose coral, *Siphonophrentis gigantea* (Leseuer, 1821) is a common constituent of Devonian carbonate deposits in the Great Lakes region of North America (e.g., Stewart, 1938; Stumm, 1965; Babcock, 1996 and references therein; McCall, 2018). In the Devonian of Ohio, coralla ranging up to 75 cm have been reported (Babcock, 1996). McCall (2018) attributed the large size of *S. gigantea* from the Lucas Formation of southwestern Ontario, Canada, to life in "deep, cold water, with access to large amounts of biological debris and nutrients." The author evidently overlooked previous work based on field observations in the Columbus Limestone of central Ohio, which demonstrated that *S. gigantea* lived recumbent in narrow, shallow channels between carbonate buildups (reefs), with the polyps facing into oncoming currents (Judge et al., 2004). The broad, shallow water carbonate platform stretching across Ohio, Ontario, and adjacent areas was located in the tropics, about 20ºS, during the Early to Middle Devonian (Scotese and Denham, 1988; Coogan, 1996; Babcock, 2009). The large size of *S. gigantea* suggests the possibility that it may have had a commensal relationship with dinoflagellate algae (contra McCall, 2018, who discounted the possibility of commensal relationships in Paleozoic rugose corals).

GEOLOGIC SETTING

Specimens used in this study are from the Columbus Limestone (Devonian: Emsian-Eifelian) of central and northwestern Ohio, including the Lake Erie islands. The Columbus Limestone represents a shallow, warm, carbonate platform environment (e.g., Babcock, 1996; Coogan, 1996; Judge et al., 2004). Various facies are represented, including coral-stromatoporoid reefs, level-bottom carbonate muds, and low-lying carbonate islands (Judge et al., 2004). More than 70 species of organisms have been recorded from the Columbus Limestone (Stewart, 1938; Stumm, 1965; Feldmann and Hackathorn, 1996). During the Emsian and Eifelian ages, much of eastern Laurentia was a passive margin, with broad, shallow carbonate platforms extending to the west, across the Great Lakes region (present-day coordinates). Beginning in the Givetian Age, collisional events in the Acadian orogenic zone led to basin subsidence and progressive collapse of the carbonate platform environments (e.g., Babcock, 2009).

METHODS

Field Work and Museum Specimens

Some specimens used in this work were collected from exposures of Columbus Limestone at Griggs Reservoir, just below the dam, along the Scioto River, Columbus Ohio. Specimens collected at the site include *Heterophrentis*, *Heliophyllum*, and *Siphonophrentis*.

Additional studied specimens of *Siphonophrentis* are from the collections of the Orton Geological Museum, The Ohio State University (prefixed OSU), and include one that was previously illustrated (e.g., Babcock, 1996, fig. 7-6.12). Prior to selecting *Siphonophrentis* specimens for XCT scanning, specimens of varied species were examined for suitability for further study, but growth banding seemed to be most obvious in *S. gigantea*.

Preliminary Analysis

Some promising specimens were sanded using a 120V Chicago Rotary Tool, and then polished using 80, 600, and 800 grit sandpaper, to reveal the internal structures including growth bands. These specimens were subsequently studied under a Bausch & Lomb Stereo Zoom microscope (10x -70x magnification) to determine the quality of preservation of growth banding. Microscopic examination indicated that the best candidates for further study were specimens of *Siphonophrentis*. Additional specimens of *Siphonophrentis gigantea* were then borrowed for study from the OSU collection. In total, 10 specimens of *S. gigantea* were selected for further analysis of density growth banding.

XCT Scanning

The *Siphonophrentis* specimens chosen for further analysis were scanned using X-ray Computed Tomography (XCT). The use of XCT provides a nondestructive method of viewing growth banding in specimens. A Neurologica CereTom CT scanner (Figure 1), housed at The Ohio State University, was used to complete the scans. Each specimen was scanned at the maximum resolution of 0.5 x 0.5 x 0.625 mm at a voltage of 120 kV (see Vayda, 2019).

Figure 1: Neurolgica CereTom CT Scanner at The Ohio State University

Measurements and Analysis

Fiji software was used to interpret and analyze the scan data. Fiji, an extension of ImageJ, allows for slice-by-slice analysis of each specimen. ImageJ, an online software that analyzes scan data, was also used to make measurements of the growth density banding present.

An average length of the growth density bands was determined and used later in χ^2 analyses. χ^2 allows for each measurement to be compared to an expected growth value, the average, to determine deviations from the norm. The χ^2 analysis is the summation of the observed values (O), measured from scan data, minus the expected value (E), the average, which is squared and divided by the expected value. The equation notation of χ^2 is:

$$\chi^2 = \sum \frac{(O - E)^2}{E}$$

The χ^2 analysis is a goodness of fit test, which is used to determine if data observed fits in a normal distribution (Metzger, 2018). A normal distribution is assumed in natural species.

RESULTS

Preservation of Specimens and Growth Banding

Ten specimens of the rugose coral *Siphonphrentis gigantea* were subjected to longitudinal XCT scans. Of them, five showed growth banding that was discernable from the scans, and the other five lacked growth banding discernable from the scans. Scanned specimens had varying degrees of internal preservation ranging from well-preserved growth banding, identified by contrasting high density/low density signatures (Figure 2), through fully recrystallized and overprinted skeletal structure, indicated by scans of near-uniform density (Figure 7). Specimens that had measurable growth banding were OSU 3854A (Figure 2), 3848 (Figure 3), 14003 (Figure 4), 17715 (Figure 5), and 47428A (Figure 6). On specimens OSU 14003 and 47428A, banding was difficult to measure in some areas because of differential recrystallization of skeletal material. Specimens that showed little or no obvious growth banding were OSU 3854B (Figure 7), 3854C, 3854D, 5517, and 47428B.

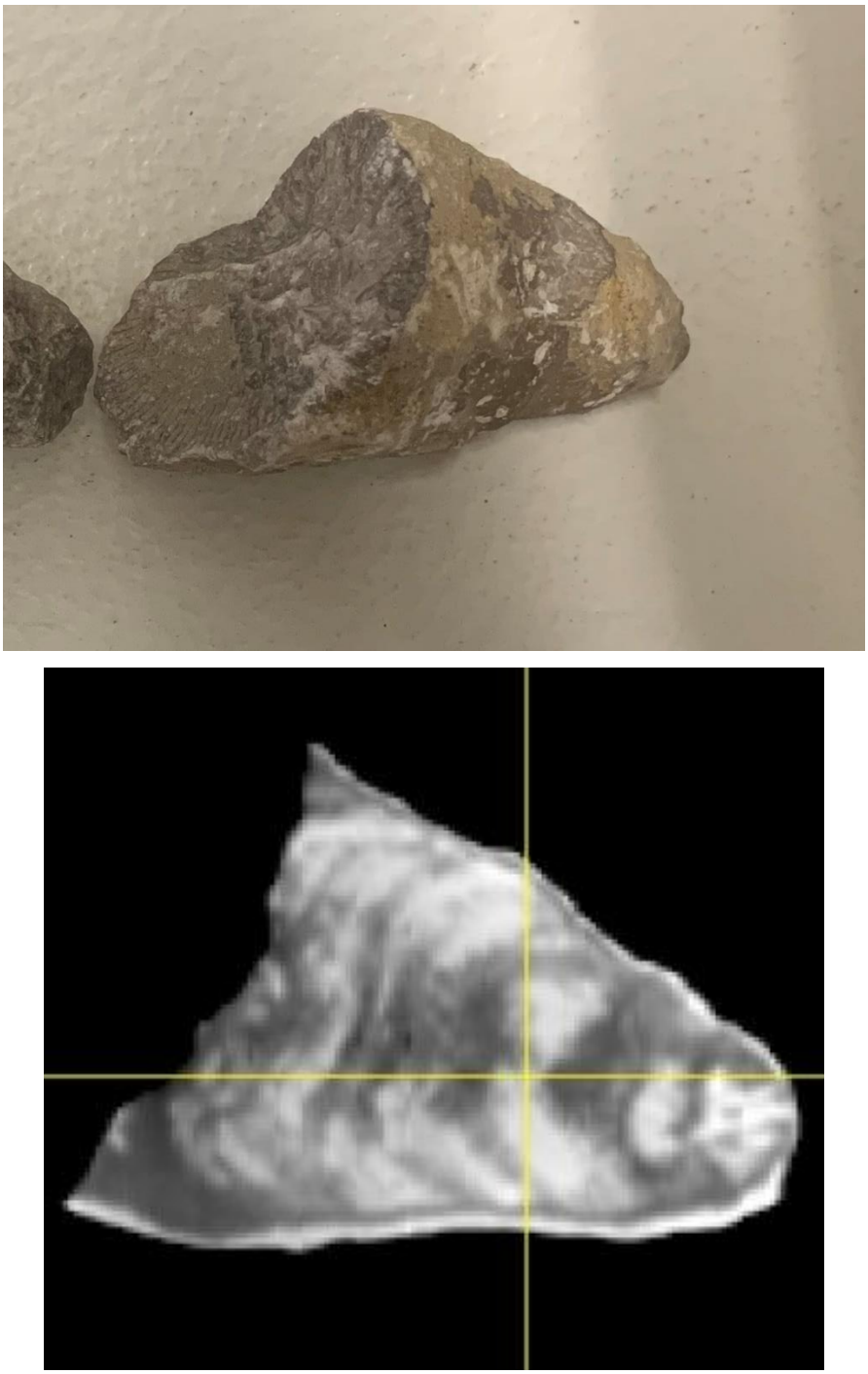

Figure 2: Siphonophrentis gigantea, *OSU 3854A, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimens, length 8.1 cm; B, longitudinal XCT scan showing well-preserved growth banding indicated by high density (light colored) and low density (dark colored) areas.*

Figure 3: Siphonophrentis gigantea*, OSU 3848, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimens, length 18.3 cm; B, longitudinal XCT scan showing well-preserved growth banding indicated by high density (light colored) and low density (dark colored) areas.*

Figure 4: Siphonophrentis gigantea, *OSU 14003, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimens, length 20.3 cm; B, longitudinal XCT scan showing well-preserved growth banding indicated by high density (light colored) and low density (dark colored) areas.*

Figure 5: Siphonophrentis gigantea*, OSU 17715, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimens, length 28.7 cm; B, longitudinal XCT scan showing well-preserved growth banding indicated by high density (light colored) and low density (dark colored) areas.*

Figure 6: Siphonophrentis gigantea, *OSU 47428A, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimens, length 19.7 cm; B, longitudinal XCT scan showing well-preserved growth banding indicated by high density (light colored) and low density (dark colored) areas.*

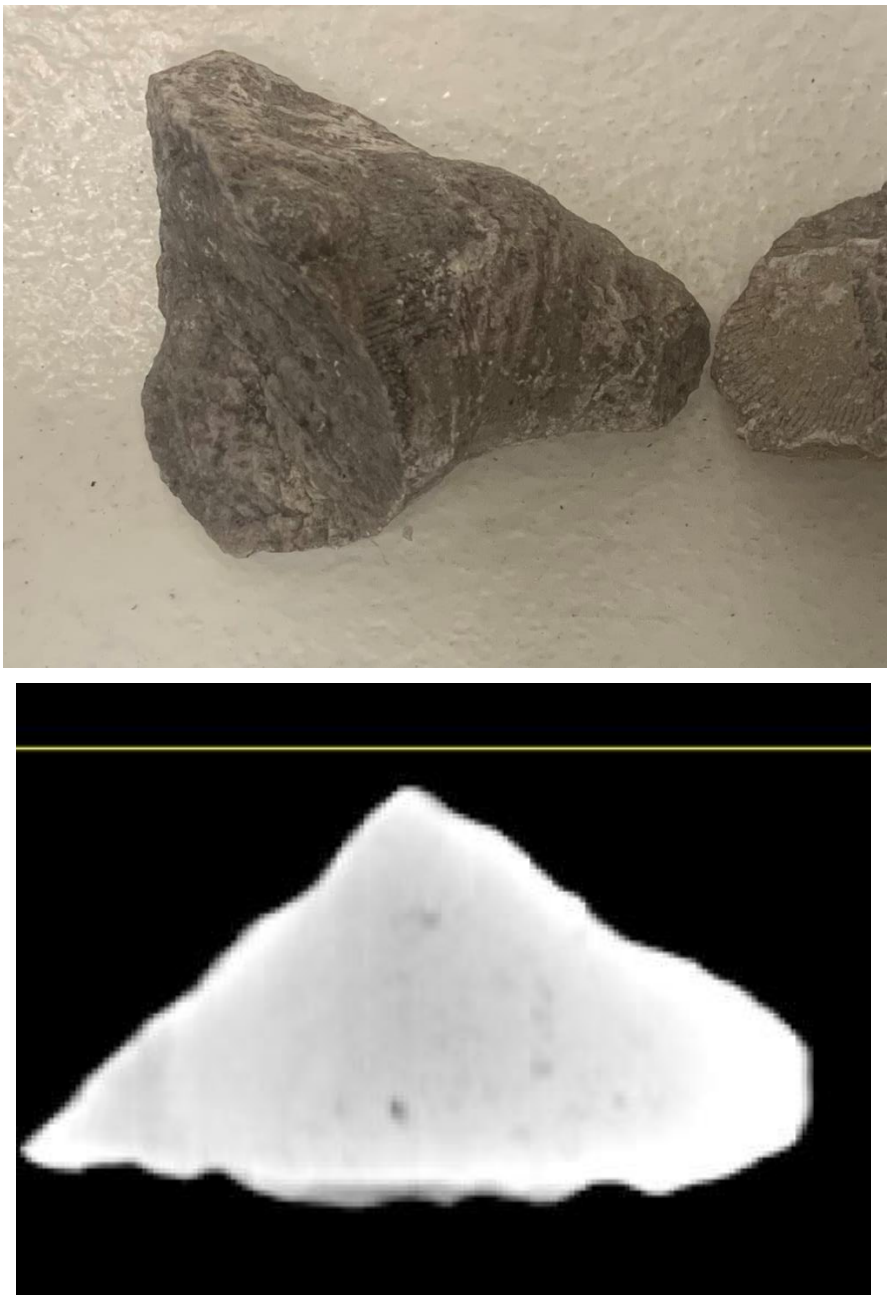

Figure 7: Siphonophrentis gigantea*, OSU 3854B, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimens, length 8.0 cm; B, longitudinal XCT scan showing little evidence of preserved growth banding; scan appears to have near-uniform density.*

Lengths of Growth Bands

Growth bands were measured from XCT scans using standardized pixel dimensions. Each pixel occupies a space equivalent to 0.49475 mm x 0.49475 mm. One growth band, inferred to represent one year's growth, is represented by a high-density/low-density couplet as viewed in longitudinal section.

Measurements of growth bands are listed in Table 1. The distribution of lengths of the growth bands are shown in Figure 8. Specimen OSU 3854A has nine measurable growth bands along a total measured length of 73.223 mm and yields an average growth rate of 8.1359 $mmyr^{-1}$. Specimen OSU 47428A has 11 measurable growth bands along a total measured length of 72.728 mm, yielding an average growth rate of 6.6117 $mmyr^{-1}$. Specimen OSU 17715 has 12 measurable growth bands along a total measured length of 129.12 mm, yielding an average growth rate of 10.759 $mmyr^{-1}$. OSU 3848 has the greatest number of measured growth bands, 18, along a total measurable length of 126.63 mm, with an average growth rate of 7.0348 $mmyr^{-1}$. OSU 14003 has the fewest measured growth bands, five, along a total measured length of 62.339 mm, yielding an average growth rate of 12.468 $mmyr^{-1}$.

Table 1: Lengths of measured growth bands in specimens of Siphonophrentis gigantea *from the Columbus Limestone (Devonian) of Ohio. All measurements are calculated from pixel lengths and given in mm.*

Growth Band #	OSU 3854A O (Observed)	OSU 47428A	OSU 17715	OSU 3848	OSU 14003
1	7.9160 mm	5.4422 mm	13.8530 mm	3.9580 mm	13.358 mm
2	6.9265 mm	6.4317 mm	12.865 mm	4.4527 mm	11.379 mm
3	10.389 mm	6.926 mm	3.9580 mm	5.4422 mm	14.842 mm
4	7.9160 mm	6.926 mm	8.9055 mm	6.9265 mm	12.863 mm
5	10.389 mm	8.4107 mm	8.9055 mm	9.8950 mm	9.8950 mm
6	11.379 mm	11.874 mm	10.884 mm	6.4317 mm	
7	7.4212 mm	6.9265 mm	12.865 mm	9.8950 mm	
8	5.9370 mm	6.4317 mm	11.874 mm	10.884 mm	
9	4.9475 mm	5.4422 mm	6.9265 mm	11.874 mm	
10		4.4527 mm	14.842 mm	4.4527 mm	
11		3.4632 mm	15.832 mm	4.4527 mm	
12			7.4062 mm	7.4062 mm	
13				8.9055 mm	
14				6.9265 mm	
15				7.4062 mm	
16				5.4422 mm	
17				6.4317 mm	
18				5.4422 mm	
Total	73.223 mm	72.728 mm	129.11 mm	126.62 mm	62.338 mm
Average	8.1358 mm	6.6116 mm	10.759 mm	7.0347 mm	12.467 mm

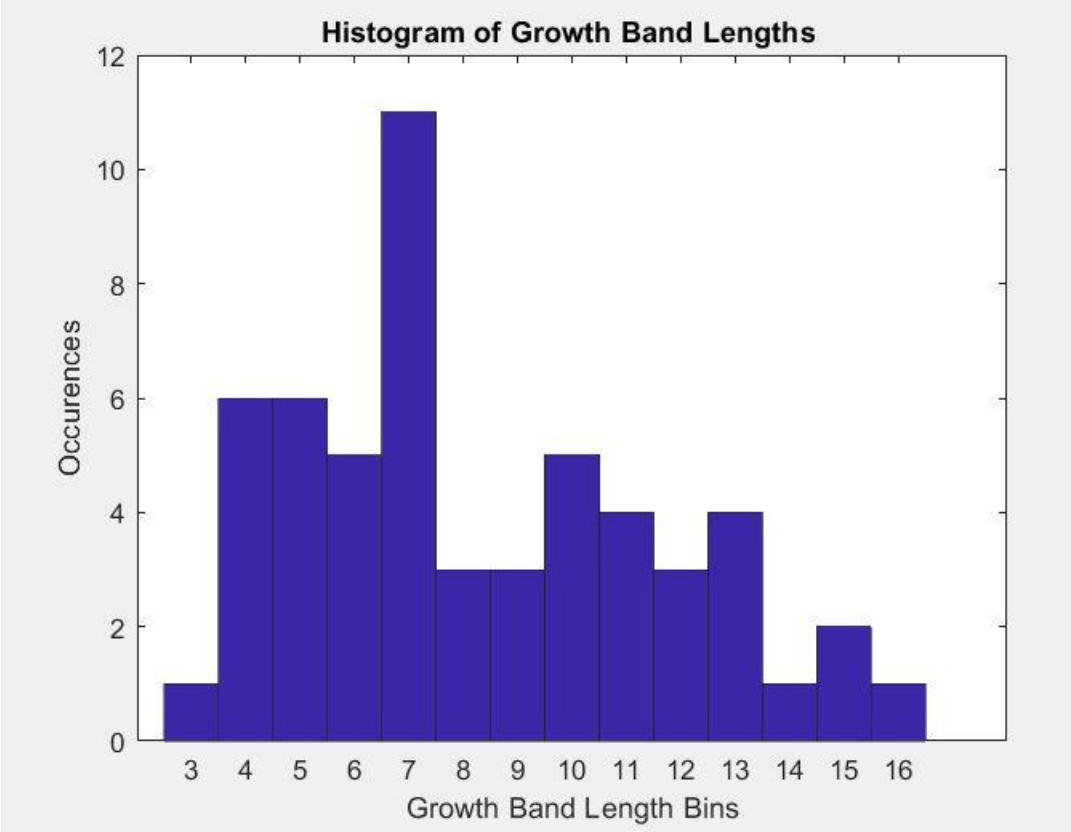

Figure 8: Distribution of growth band lengths measured from specimens of Siphonphrentis gigantea*, Columbus Limestone (Devonian), Ohio.*

χ^2 Analysis of Specimens

A χ^2 analysis on growth bands lengths was performed for each of the five specimens that showed measurable banding. The null hypothesis is that growth band lengths in *Siphonphrentis gigantea* are due to chance. The alternative hypothesis is that growth band lengths in *S. gigantea* are not due to chance, meaning that something else explains the distribution of their lengths. Results of the χ^2 tests are provided in Tables 2-6.

To determine if the null hypothesis could be accepted or rejected, a p-value was assigned to each specimen based on the number of growth bands that were measurable. The p-value for this experiment is 0.05, so any value less than this fails to reject the null hypothesis. Degrees of freedom (df) were calculated as: number of growth bands -1. In Tables 2-6, O symbolizes the Observed Value, the measured length of each growth band. The Expected Value (E) for the length of a growth band is the average growth band length of all measured specimens. The value of E was determined to be 8.347 mm. Specimen OSU 47428A has 11 measurable growth bands, yielding10 degrees of freedom (df). With a p-value of 0.05, the critical value (CV) of this specimen is 18.307. Table 2 shows that OSU 47428A has a χ^2 of 10.104, which is less that the CV. The null hypothesis is not rejected. Specimen OSU 3854A has 9 measurable growth bands, yielding 8 df. The CV for this specimen is 15.507. The χ^2 value calculated for OSU 3854A (Table 3) is 4.5710, which is less than the CV. The null hypothesis is not rejected.

Specimen OSU 47428A has 11 measurable growth bands, yielding10 degrees of freedom (df). With a p-value of 0.05, the critical value (CV) of this specimen is 18.307. Table 2 shows that OSU 47428A has a χ^2 of 10.104, which is less that the CV. The null hypothesis is not rejected.

Specimen OSU 3854A has 9 measurable growth bands, yielding 8 df. The CV for this specimen is 15.507. The χ^2 value calculated for OSU 3854A (Table 3) is 4.5710, which is less than the CV. The null hypothesis is not rejected.

Specimen OSU 17715 has 12 measured growth bands, yielding 11 df. The CV for this specimen is 19.675. The χ^2 value calculated for OSU 3854A (Table 4) is 24.406, which is greater than the CV. The null hypothesis is rejected.

Specimen OSU 3848 has 18 measured growth bands, yielding 17 df. The CV for this specimen is 27.587. The χ^2 value calculated for OSU 3848 (Table 5) is 15.597, which is less than the CV. The null hypothesis is not rejected.

Specimen OSU 14003 has 5 measured growth bands, yielding 4 df. The CV for this specimen is 9.4877. The χ^2 value calculated for OSU 14003 (Table 6) is 11.334, which is greater than the CV. The null hypothesis is rejected.

Table 2: χ^2 analysis of growth bands lengths in Siphonphrentis gigantea*, OSU 47428A. The critical value is 18.307 .*

O (observed)	O-E	$(O-E)^2$	$(O-E)^2/E$	χ^2
5.4422	-2.9947	8.9685	1.0629996	10.104
6.4317	-2.0052	4.0210	0.47659	
6.9265	-1.5105	2.2816	0.27042	
6.9265	-1.5105	2.2816	0.27042	
8.4107	-0.026250	0.00068910	8.167E-05	
11.874	3.4370	11.812	1.4001	
6.9265	-1.5105	2.2816	0.27042	
6.4317	-2.0052	4.0210	0.47659	
5.4422	-2.9947	8.9685	1.0629	
4.4527	-3.9842	15.874	1.8815	
3.4632	-4.9737	24.738	2.9321	

Table 3: χ^2 analysis of growth bands lengths in Siphonphrentis gigantea, *OSU 3854A. The critical value is 15.507 .*

O (observed)	O-E	$(O-E)^2$	$(O-E)^2/E$	χ^2
7.9160	-0.52100	0.27144	0.0321727	4.5710
6.9265	-1.5105	2.2816	0.27042	
10.389	1.9527	3.8132	0.45196	
7.9160	-0.52100	0.27144	0.032172	
10.389	1.9527	3.8132	0.45196	
11.379	2.9422	8.6568	1.0260	
7.4210	-1.0157	1.0317	0.12228	
5.9370	-2.5000	6.2500	0.74078	
4.9475	-3.4895	12.176	1.4432	

Table 4: χ^2 analysis of growth bands lengths in Siphonphrentis gigantea, *OSU 17715. The critical value is 19.675 .*

O (observed)	O-E	$(O-E)^2$	$(O-E)^2/E$	χ^2
13.853	5.416	29.333	3.4767	24.406
12.865	4.4283	19.609	2.3242	
3.9580	-4.4790	20.061	2.3777	
8.9055	0.4685	0.21949	0.026015	
8.9055	0.4685	0.21949	0.026015	
10.884	2.4475	5.9902	0.70999	
12.865	4.4283	19.609	2.3242	
11.874	3.4370	11.812	1.4001	
6.9265	-1.5105	2.2816	0.27042	
14.842	6.4055	41.030	4.8631	
15.832	7.3950	54.686	6.4816	
7.4062	-1.0307	1.0624	0.12592	

Table 5: χ^2 analysis of growth bands lengths in Siphonphrentis gigantea, *OSU 3848. The critical value is 27.587 .*

O (observed)	O-E	$(O-E)^2$	$(O-E)^2/E$	χ^2
3.9580	-4.4790	20.061	2.3777	15.597
4.4527	-3.9842	15.874	1.8815	
5.4422	-2.9947	8.9685	1.0629	
6.9265	-1.5105	2.2816	0.27042	
9.8950	1.4580	2.1257	0.25195	
6.4317	-2.0052	4.0210	0.47659	
9.8950	1.4580	2.1257	0.25195	
10.884	2.4475	5.9902	0.70999	
11.874	3.4370	11.812	1.4001	
4.4527	-3.9842	15.874	1.8815	
4.4527	-3.9842	15.874	1.8815	
7.4062	-1.0307	1.0624	0.12592	
8.9055	0.46850	0.21949	0.026015	
6.9265	-1.510	2.2816	0.27042	
7.4062	-1.0307	1.0624	0.12592	
5.4422	-2.9947	8.9685	1.0629	
6.4317	-2.0052	4.0210	0.47659	
5.4422	-2.9947	8.9685	1.0629	

Table 6: χ^2 analysis of growth bands lengths in Siphonphrentis gigantea, *OSU 14003. The critical value is 9.4877 .*

O (observed)	O-E	$(O-E)^2$	$(O-E)^2/E$	χ^2
13.358	4.9212	24.218	2.8705	11.334
11.379	2.9422	8.6568	1.0260	
14.842	6.4055	41.030	4.8631	
12.863	4.4265	19.593	2.3223	
9.8950	1.4580	2.1257	0.25195	

Discussion

χ^2 Results

The χ^2 analyses performed on specimens with measurable growth bands showed that two specimens (OSU 14003, 17715) of the five analyzed had χ^2 values greater than their respective critical p-values. For these two specimens, the null hypothesis is rejected and the alternative hypothesis is accepted. The alternative hypothesis is that something other than normal growth rate played a role in the growth rate. These two specimens are among the largest that were scanned with the XCT. OSU 14003 measures 20.3 cm in length, and OSU 17715 measures 28.7 cm in length. Both specimens showed growth rates exceeding the expected rate, based on the average of all measured growth intervals.

What factors might have increased the growth rate of these corals? Possible explanations include 1, internal factors such as the presence of zooxanthellate endosymbionts; and 2, various external environmental factors.

The first factor to consider with these corals is the possibility that they harbored a zooxanthellate endosymbiont. *Siphonophrentis* is the largest solitary rugose coral known from Ohio; individual coralla reach up to 75 cm in length (Babcock, 1996). To reach such large sizes, having endosymbionts seems reasonable. Zooxanthellate corals from the Holocene can reach large sizes and have high growth rates, ranging anywhere from 5-10 $mmyr^{-1}$ to 150 $mmyr^{-1}$ (Dullo, 2005). Judge et al. (2004) provided cogent evidence that *Siphonophrentis* laid in shallow channels between carbonate buildups (reefs), all facing the incoming current. The carbonate buildups stood 1 to 2 m above the bases of the adjacent channels. This would mean that *Siphonophrentis* lay recumbent in water that was about 2 to 4 m deep. Extant corals of the Caribbean that are deeper water have a growth rate near 10 $mmyr^{-1}$ (Dullo, 2005); this coulod be viewed as a baseline for comparison with the growth rate of *S. gigantea*. The large size of *Siphonophrentis* and its inferred habitat open the possibility that it harbored zooxanthellate endosymbionts.

External environmental factors also influence the growth rates of corals. Most notable among the factors recognized from Holocene carbonate platform settings are light levels, water temperature, sea level, and suspended particles (Dullo, 2005). The size and high growth rate of at least some *Siphonophrentis* specimens could have been related to favorable external conditions including some or all of these. During the Early (Emsian) to early Middle Devonian (Eifelian), the present-day eastern-midwestern region of ancestral North America was a passive margin to carbonate platform, sea level was relatively high, and present-day Ohio was located in the tropics south of the Equator (Wiedman, 1988; Babcock, 2009). If external environmental factors are the source of the large size of some *Siphonophrentis*, the implication would be that light levels are not as important because the coral would not be wholly reliant on photosynthesis in a symbiont for food.

Variability of Preservation Quality

There is considerable variability in the quality of preserved coral skeleton in the Columbus Limestone. Prior to selecting specimens for XCT scanning, >50 coral specimens housed in the Orton Geological Museum, of varied species, were examined for suitability for further study. Most specimens show some degree of silicification (see Babcock, 1996), a process in which calcium carbonate skeleton is replaced by silica. Scoffin (1992) described the taphonomic process of silicification of corals as direct precipitation through cellular voids or as replacement of skeletal calcium carbonate. Silicification can change the density of coral skeleton and can destroy the internal density of growth banding. *Siphonophrentis* built its skeleton of calcium carbonate (presumably aragonite), which makes it susceptible to silicification. Ultimately, the specimens selected for XCT scanning comprise a subset of the available specimens of *S. gigantea*, ones that appeared to have little to no silicification.

Preservational differences among the studied specimens had an impact on the results. The better preserved specimens were those with little or no silicification. In these well-preserved specimens, is, growth banding tended to be preserved, and accurate measurements could be made from XCT scans. Five of the 10 scanned specimens did not have well preserved or measurable growth banding, inferred to be the result of silicification that was not readily apparent from external examination. One example, OSU 3854C, is shown in Figure 9.

Two specimens that had measurable and preserved growth banding but also preservation anomalies were OSU 47428A and OSU 3848. OSU 3848 (Figure 10) had measurable growth banding, but it was difficult to see except by pixel by pixel analysis of the scans. In this specimen there is a strange area of low density within the inner parts of the skeleton that does not align with growth bands. This could be due to silicification in certain zones of the specimen (compare Rodriguez, 2004). OSU 47428A has several small areas of exceptionally low density, probably large pore spaces, internal to the fossil. These anomalies could be due to dissolution, a taphonomic process in which parts of a skeleton are dissolved due to chemical reactions (Scoffin, 1992). These pores also might be related in part to growth abnormalities, as it appears that some growth bands circumvent the pores (Figure 11).

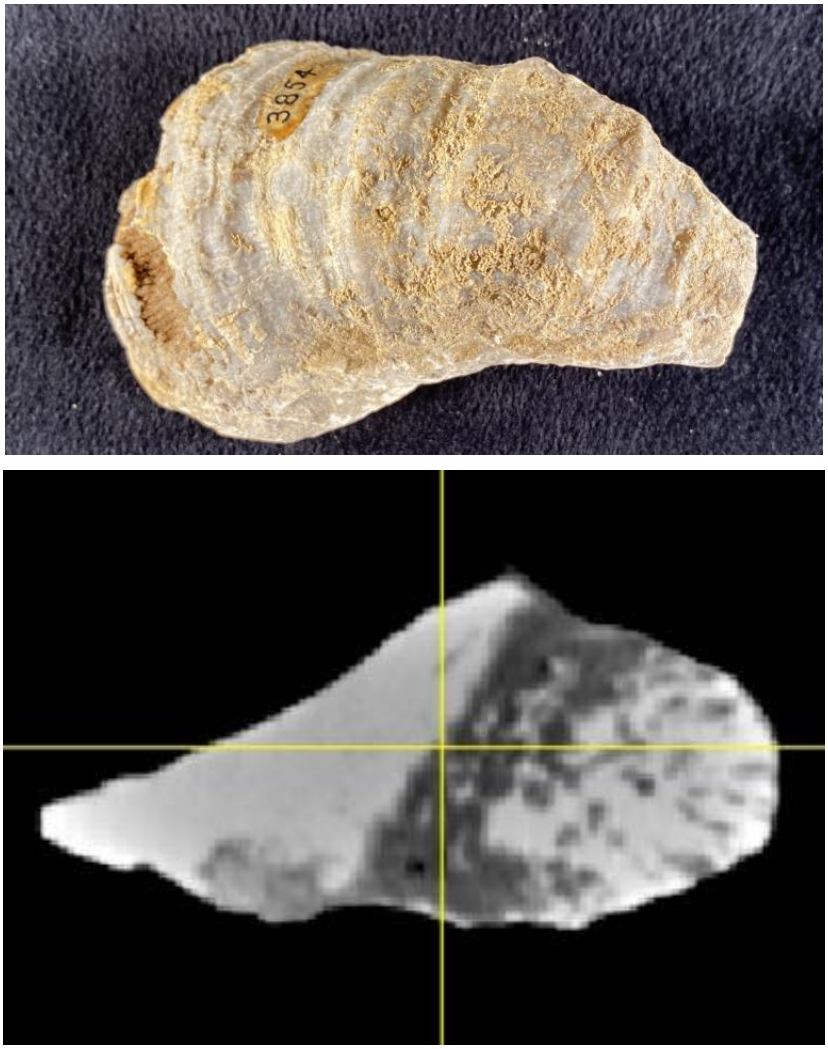

Figure 9: Siphonophrentis gigantea*, OSU 3854C, Columbus Limestone (Devonian), Franklin County, Ohio; A, external view of specimen, length 10.8 cm; B, longitudinal XCT scan showing little evidence of preserved growth banding, inferred to be the result of silicification.*

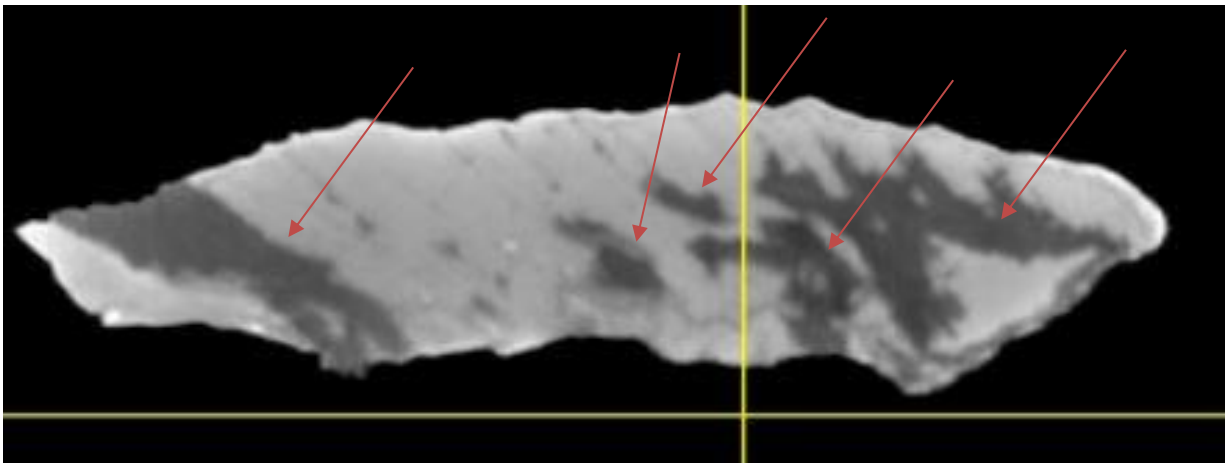

Figure 10: Siphonophrentis gigantea, *OSU 3848, longitudinal XCT scan showing anomalous low density areas (arrows) affecting preservation of complete density growth bands.*

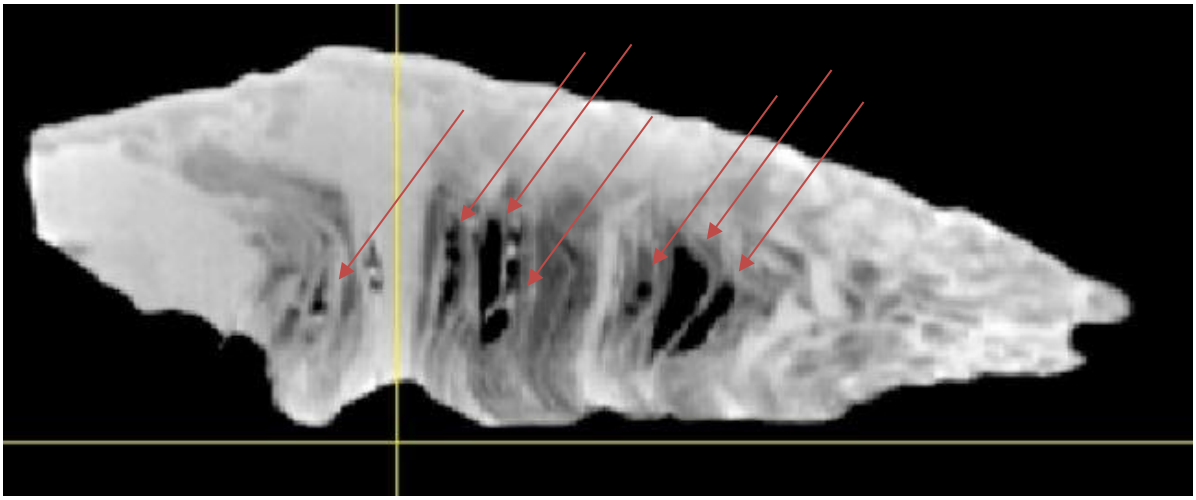

Figure 11: Siphonophrentis gigantea, *OSU 47428A, longitudinal XCT scan showing exceptionally low density areas (arrows), inferred pore spaces, internally.*

Possible Bleaching Event

One of the main goals of this study was to search for possible bleaching events preserved via the growth banding of *Siphonophrentis*. Good evidence of bleaching would provide further support for the hypothesis that *Siphonophrentis* was a zooxanthellate coral. One studied specimen shows a distinct interruption to the normal growth banding, which could have been related to bleaching. In OSU 17715 (Figure 12) a growth band that is considerably narrower than any other band surrounding it indicates a short-term, but significant, reduction in growth rate (compare Leder et al., 1990). The narrow growth band is 3.958 mm in length. For comparison, the average width of growth bands in this this specimen is 10.759 mm. This specimen also had a χ^2 value greater than its critical p-value, suggesting that something altered its growth rate.

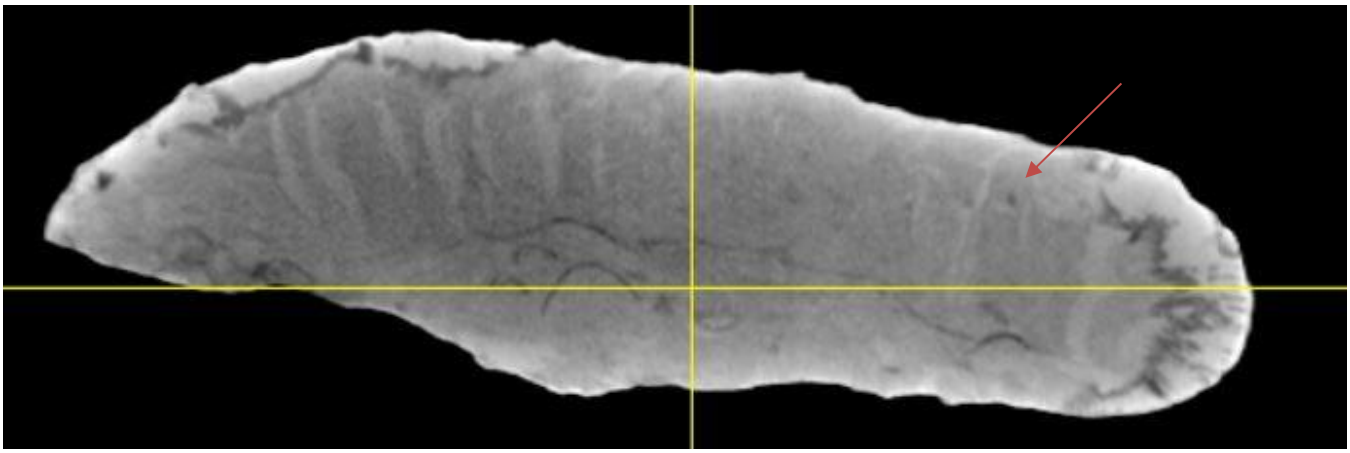

Figure 12: Siphonophrentis gigantea, OSU 17715, longitudinal XCT scan showing narrow growth band (3.958 mm, arrow), which is approximately one-third the average width of a growth band in this specimen.

CONCLUSIONS

This study had three major objectives: 1, to determine if corals from the Columbus Limestone (Devonian) of Ohio preserved internal growth banding; 2, to determine if the large *Siphonophrentis* was a zooxanthellate coral; and 3, to seek evidence for environmental perturbations, such as bleaching events, in the skeletal records of *Siphonophrentis*.

Well-preserved growth banding was observed, through standard observation (in some examples) and in XCT scans, in five specimens of *S. gigantea*.

Analysis of growth band widths suggests that in at least two of five measured specimens' growth rate was greater than expected. That, together with overall large size of the corallum, is consistent with the hypothesis that *S. gigantea* harbored photosynthetic zooxanthallae symbionts.

One studied specimen showed marked disruption along one growth band. The greatly reduced growth rate was likely due to some environmental perturbation. The disrupted growth band resembles growth bands in Holocene corals that have experienced bleaching events, in which algal symbionts have exited the coral polyp. If indeed the reduced growth rate reflects an ancient bleaching event, this would further support the hypothesis that *Siphonophrentis* was a zooxanthellate coral. More data are needed to confirm the hypothesized relationship of a rugose coral-zooxanthellae symbiosis, but the data presented here are promising.

RECOMMENDATIONS FOR FUTURE WORK

The most important next steps for work regarding this thesis is to expand the total number of specimens XCT scanned. This step would provide more data to pull from and provide a wider view of the diversity within *Siphonophrentis*. Another method that could be used in conjunction with XCT would be to do isotopic analyses of the specimens. Analyses of $\delta^{13}C$ and $\delta^{18}O$ could provide chemical information that could be compared with known zooxanthellate and nonzooxanthellate corals (Stanley and Swart, 1995). Similar work on Paleozoic tabulate would be useful for providing insight into the evolution of coral-zooxanthellae symbioses. Work could be done on Ordovician and Silurian material to extend information on the timing of early coral-dinoflagellate symbiosis. Work also could be expanded to areas such as New York, Indiana, Michigan, and Ontario, where preservation in carbonate deposits of equivalent age may be better.

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